

OBSERVATIONS ON POLYPLOIDY IN *FUCHSIA* SECTS. *QUELUSIA* AND *KIERSCHLEGERIA* (ONAGRACEAE)¹

Takuji Hoshino² and Paul E. Berry³

ABSTRACT

Chromosome numbers are reported for all eleven taxa currently recognized in Fuchsia sect. Quelusia and for F. lycioides, the sole member of sect. Kierschlegeria. Results are based on the study of individuals from 103 native populations and 13 cultivated plants. Most species and sections of Fuchsia are diploid (n = x = 11), but sects. Quelusia and Kierschlegeria are entirely polyploid, including the only naturally occurring octoploids in the genus. Polyploidy in these sections is always associated with 3(4)-aperturate pollen grains, instead of the normal 2-aperturate condition in the genus. All chromosome counts obtained from F. lycioides and from seven of the nine species in sect. Quelusia were tetraploid, but intraspecific variation in ploidy level was found in two Brazilian species of sect. Quelusia. The only wild individual examined of F. alpestris was tetraploid, whereas a cultivated specimen of this species from Europe was octoploid. In the widespread, polytypic F. regia, all individuals examined of subspecies reitzii and serrae were octoploid, but both tetraploid and octoploid populations were found in subsp. regia. Both ploidy levels were also found in the extreme northern range of subsp. serrae, in individuals that were morphologically intermediate with subsp. regia. This situation suggests that octoploidy has evolved recently and possibly repeatedly in sect. Quelusia, whereas tetraploidy probably originated in a common ancestor to sects. Quelusia and Kierschlegeria.

Fuchsia is one of the largest genera of the Onagraceae, with over 100 species occurring mostly in tropical montane cloud forests. It is placed in its own tribe, Fuchsieae, on the basis of its fleshy fruits and mostly 2-aperturate pollen. Chromosomes in Fuchsia are large and are heterogeneous in size for the family, with interphase nuclei having pycnotic areas that are variable in number, size, and density (Kurabayashi et al., 1962); these are unspecialized features shared with Lopezia and Circaea. All species examined in the genus have the basic chromosome number of the family, x = 11 (Raven, 1979), and none have the translocation systems or aneuploidy that are characteristic of other onagraceous genera such as Oenothera and

sections of Fuchsia, the distribution of chromosome numbers has been determined for as many species as possible in the genus, together with extensive surveys of the palynology and foliar flavonoid chemistry of most taxa (Nowicke et al., 1984; Averett et al., 1986). To date, diploid chromosome counts (n = 11) have been obtained for 69 species and tetraploid counts (n = 22) for 10 species (Breedlove, 1969; Breedlove et al., 1982; Berry, 1982, 1985; Berry et al., 1988; Hoshino & Berry, 1988). Of the ten sections currently recognized in the genus (Berry et al., 1988), six are entirely diploid. The two largest sections, Fuchsia (61 species) and Hemsleyella (14 species), are predominantly diploid, but sect. Fuchsia has six known tetraploid or partly tetraploid species (Berry, 1982), and sect. Hemsleyella has two tetraploid species (Berry, 1985). This paper presents the results of

Clarkia.

In recent efforts to improve our understanding of the relationships of the different species and

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² Biological Laboratory, Okayama University of Science, 1-1 Ridai-Cho, Okayama 700, Japan.

³ Departamento de Biología de Organismos, Universidad Simón Bolívar, Apartado 89000, Caracas 1081, Venezuela. Current address: Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.

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TABLE 1. Summary of chromosome numbers in Fuchsia sect. Quelusia.

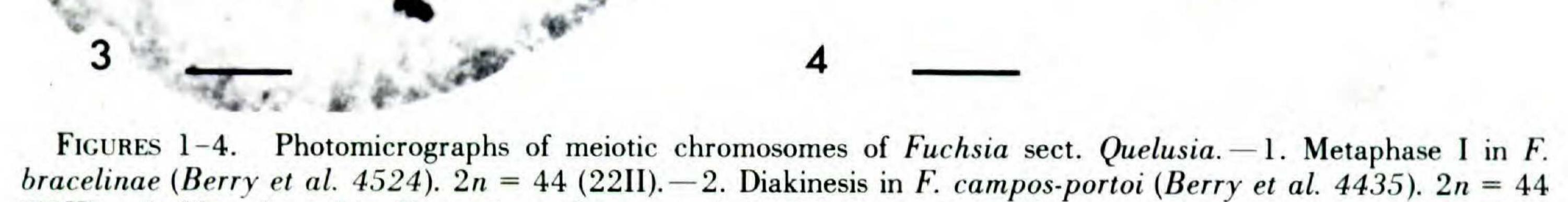
| | Gametic |
|----------------------|---------|
| | Chromo- |
| | some |
| Taxon | Number |
| F. alpestris Gardner | 22, 44 |
| F. bracelinae Munz | 22 |
| F brevilobis P Berry | 22 |

a comprehensive survey of the cytology of all 11 taxa of sect. *Quelusia*, concurrently with a systematic revision of the section (Berry, 1989). It also presents the first published counts for *Fuchsia lycioides*, the sole member of sect. *Kierschlegeria*.

The only previous reports on chromosomes in sect. Quelusia were from F. magellanica. The first report by Warth (1923) was n = 22 for F. coccinea, but photographs in a subsequent publication (Warth, 1925) showed that this was a misidentification of F. magellanica. Johanssen (1929a, b) reported diploid counts of n = 11 for two horticultural selections of F. magellanica, but no vouchers or illustrations were provided to verify the identity of his plants, which were very likely misidentified (P. Raven, pers. comm.). A report of 2n = 44 in F. magellanica by Haque (1952) also lacked vouchers. Chaudhuri (1956) made counts of n = 22 in F. magellanica and noted that it had

| r. orevitoois r. Derry | 22 |
|--------------------------------------|--------|
| F. campos-portoi Pilger & Schulze | 22 |
| F. coccinea Dryander | 22 |
| F. glazioviana Taubert | 22 |
| F. hatschbachii P. Berry | 22 |
| F. magellanica Lamarck | 22 |
| F. regia (Vellozo) Munz subsp. regia | 22, 44 |
| F. regia subsp. reitzii P. Berry | 44 |
| F. regia subsp. serrae P. Berry | 44 |
| | |



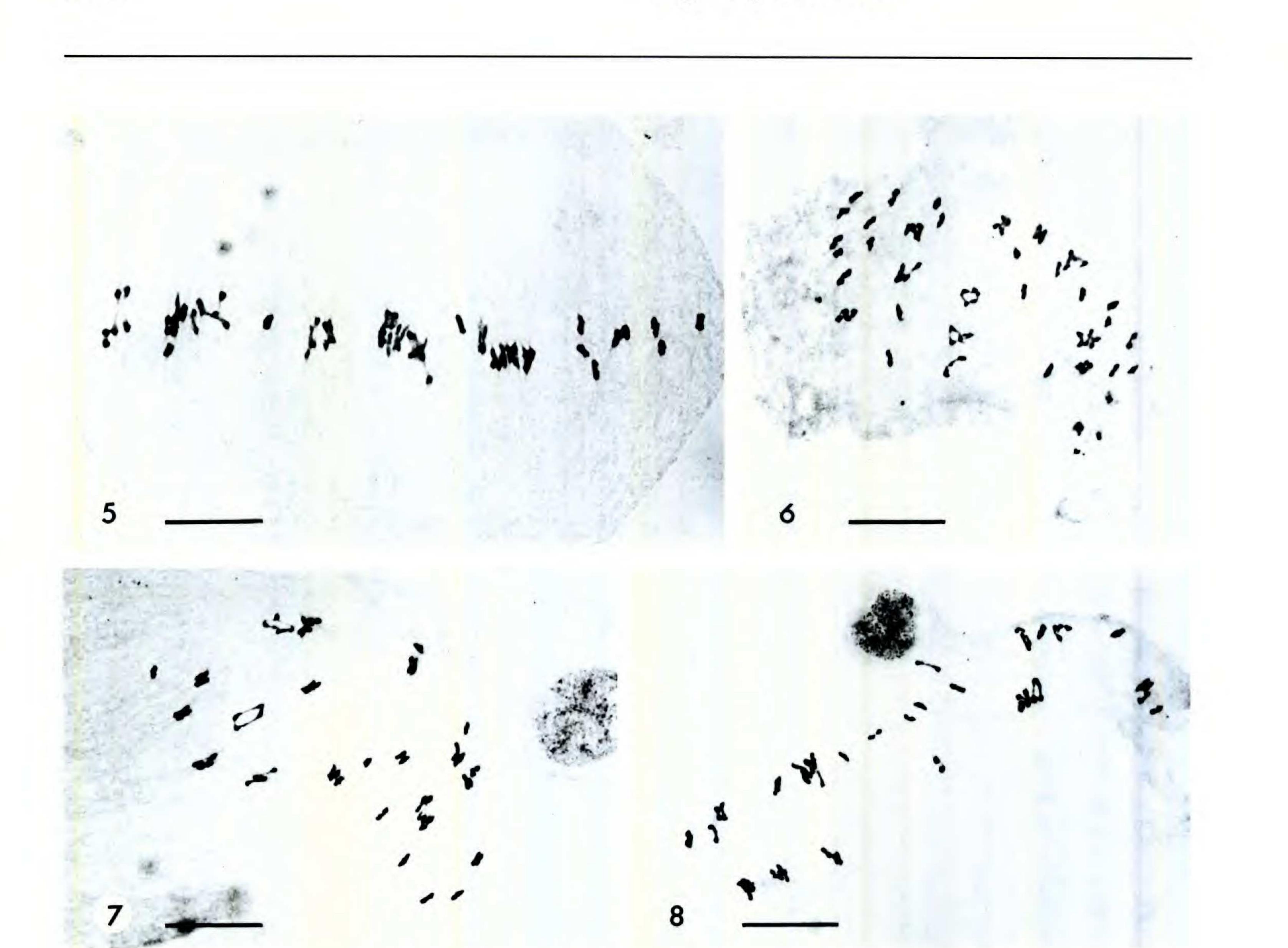


(22II). -3. Metaphase I in F. coccinea (Berry et al. 4458). 2n = 44 (22II). -4. Metaphase I in F. regia subsp. regia (Berry et al. 4544). 2n = 44 (22II). Scale bars = 10 μ m.

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FIGURES 5-8. Photomicrographs of meiotic metaphase chromosomes of Fuchsia sect. Quelusia. -5. Fuchsia regia subsp. reitzii (Berry & Falkenberg 4510). 2n = 88 (15IV & 14II). -6. Fuchsia regia subsp. serrae (Berry et al. 4492). 2n = 88 (9IV & 26II). -7. Fuchsia regia subsp. serrae (Berry et al. 4493). 2n = 88 (17IV & 10II). -8. Fuchsia regia subsp. reitzii (probable hybrid with subsp. serrae, from Berry & Falkenberg 4517). 2n = 88 (15IV & 14II). Scale bars = 20 μ m.

distinctly shorter chromosomes than several diploid species he examined in the genus. Kurabayashi et al. (1962) examined two different collections of F. *magellanica*, which they also found to be tetraploid with short chromosomes. Although Chaudhuri (1956) reported a tetraploid count for F. lycioides, no voucher specimens were provided, and his description of this entity clearly indicates that it was a hybrid, probably of F. magellanica $\times F$. lyin Carnoy's solution and macerated in 10% HCl for 6 minutes at 60°C. The root tips were stained in 1% aceto-orcein for 10 or 20 minutes and then squashed.

To establish pollen fertility, pollen grains were stained with Alexander's solution (Alexander, 1969).

RESULTS

Chromosome counts from 40 different popula-

cioides parentage.

MATERIALS AND METHODS

Meiotic chromosomes were examined in pollen mother cells of young buds fixed in Carnoy's solution (3:1 absolute ethanol to glacial acetic acid) for 24 hours, then transferred to 70% ethanol for storage. Anthers were squashed in 1% aceto-orcein.

Somatic chromosomes were studied in root tip apices, which were pretreated in 0.002 M aqueous 8-hydroxyquinoline for 6 hours at 5°C, then fixed tions of native and cultivated individuals of F. magellanica were consistently tetraploid (n = 22; Table 1, Appendix). The populations sampled covered most of the range of this widespread species of southern Argentina and Chile, leaving little doubt that it is cytologically uniform throughout its range. Counts of all other taxa in sect. Quelusia represent their first validated chromosome reports (Table 1). Seven Brazilian species, including the newly described F. brevilobis and F. hatschbachii (Berry, 1989), are all tetraploid, based on at least two counts for each species. The Chilean F. lycioides

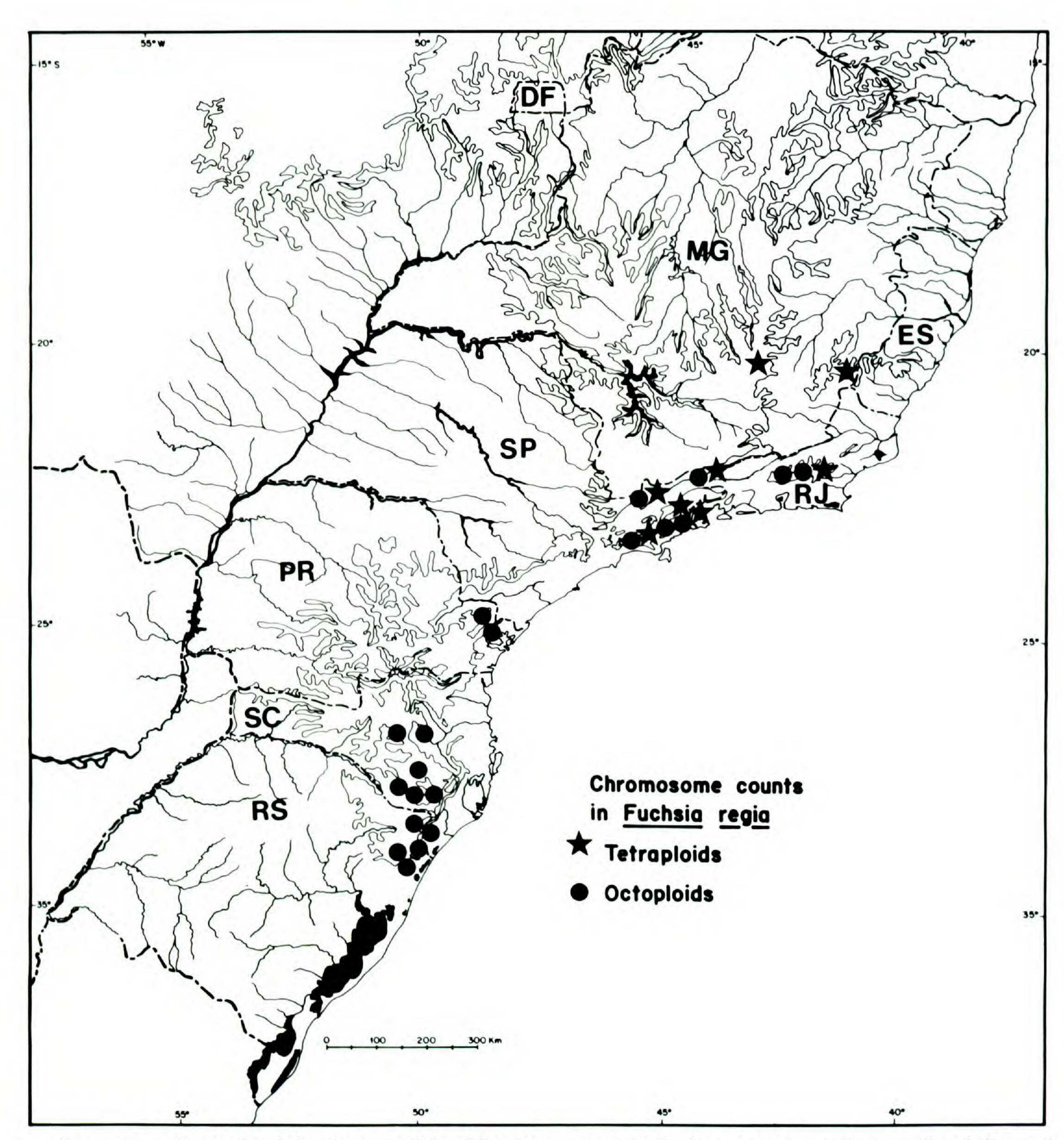


FIGURE 9. Geographical distributions of the different cytotypes of Fuchsia regia in southeastern Brazil. Pairs of capital letters refer to state abbreviations, RJ = Rio de Janeiro, etc. Contour lines indicated at 800 m.

(sect. Kierschlegeria) is also tetraploid. Normal bivalent formation was found in all tetraploid collections examined (Figs. 1-4). In the Brazilian F. alpestris, the single naturally occurring individual counted was tetraploid, but a plant of this species cultivated in Europe was octoploid.

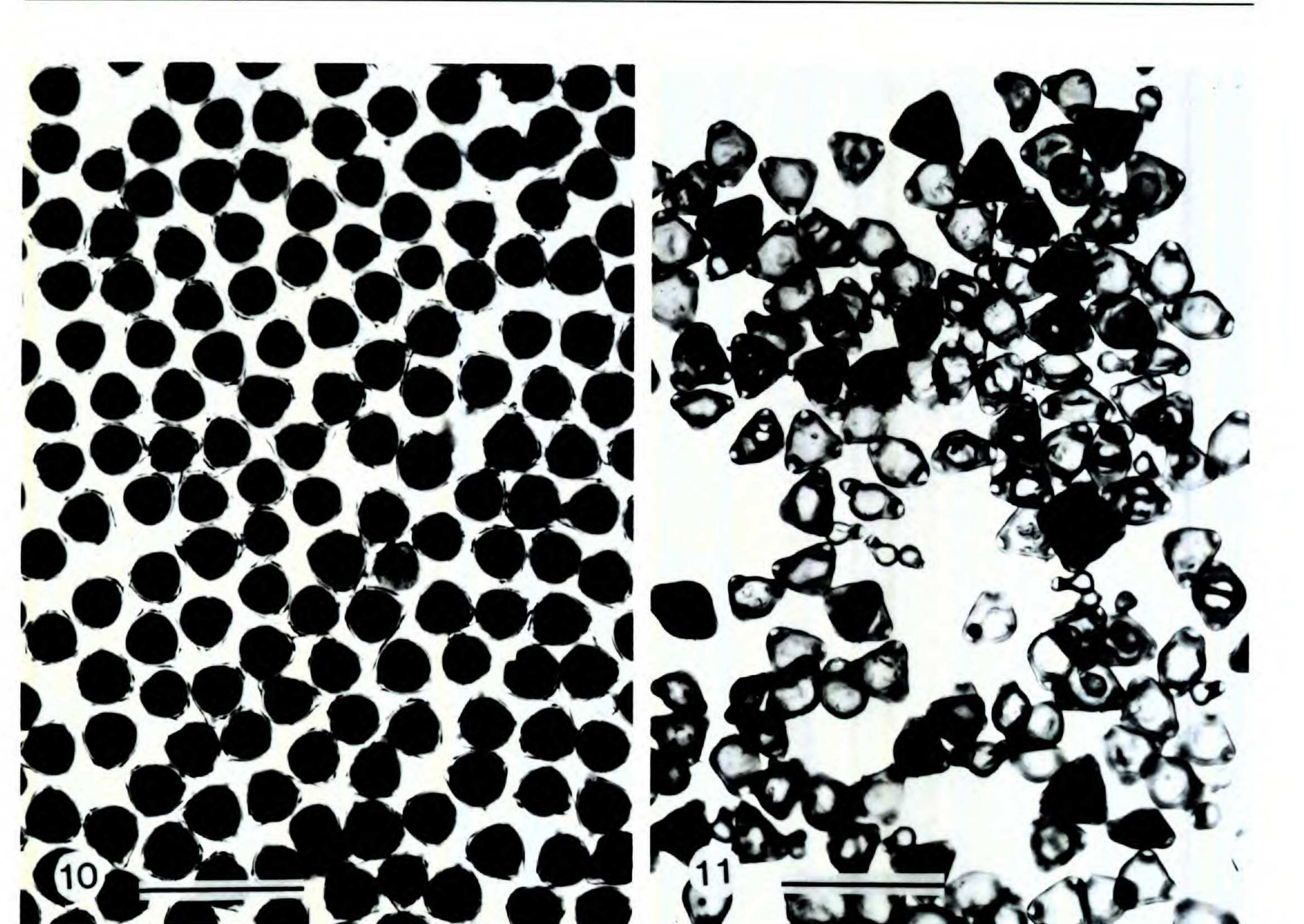
Fuchsia regia, the most widespread species of the genus in Brazil, has tetraploid and octoploid populations (see Appendix). Populations from the southern half of its range were entirely octoploid, including all populations counted of subspecies reitzii and serrae and one naturally occurring hybrid between them. In most of the octoploids, numerous quadrivalents and bivalents were formed (Figs. 5-8).

Populations of *F. regia* subsp. *regia* with both tetraploid and octoploid individuals were found in northern São Paulo and southern Rio de Janeiro states (Appendix, Figure 9). The southernmost tetraploid individuals of *F. regia* came from northcentral São Paulo State. These collections are morphologically intermediate, probable hybrids between subspecies *regia* and *serrae*. They also occurred sympatrically with octoploid individuals

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FIGURES 10, 11. Photomicrographs of pollen grains from Fuchsia sect. Quelusia. -10. Fuchsia regia subsp. serrae (2n = 88) (Ramamoorthy & Hatschbach 830). -11. Fuchsia regia subsp. regia \times F. regia subsp. serrae (2n = 66), artificial hybrid between Ramamoorthy 683 (subsp. regia, 2n = 44) and Ramamoorthy & Hatschbach 830 (subsp. serrae, 2n = 88), cultivated at Missouri Botanical Garden, M2588. Scale bars = 150 μ m.

of F. regia subsp. serrae, but no hexaploid individuals were found in these areas. In Minas Gerais and other parts of Rio de Janeiro, all populations of subsp. regia sampled were tetraploid. The distribution of the different cytotypes of F. regia is shown in Figure 9.

Although meiosis was not observed in an artificial hexaploid hybrid between a tetraploid plant of F. *regia* subsp. *regia* and an octoploid one of subsp. *serrae*, more than 50% of the pollen grains of the hybrid were aborted. Both parents, however, showed fully stained and apparently viable pollen grains (Figs. 10, 11).

preliminary chloroplast DNA restriction site analysis by Sytsma & Smith (1988) has shown the two sections to be more closely related to one another than to any other section of the genus. The results of a separate cladistic analysis of the species of these two sections by Berry (1989) were consistent with the hypothesis that tetraploidy evolved in a common ancestor. Since the other eight sections of the genus are predominantly diploid, including the South Pacific sect. Skinnera and all four Central American sections, it is clear that no existing member of sect. Quelusia or sect. Kierschlegeria could have directly given rise to those groups. Octoploidy in natural populations of Fuchsia is known only in sect. Quelusia, where it has been detected primarily in F. regia, a species that also has tetraploid populations. Quadrivalents are common in the octoploid individuals examined, indicating a close chromosomal homology between the genomes that came together. Both the presence of different ploidy levels and the varying numbers of multivalents in F. regia indicate a recent origin of octoploidy in the genus. Whether the octoploidy detected in F. alpestris originated naturally or

DISCUSSION

Sections *Kierschlegeria* and *Quelusia* are the only entirely polyploid sections of *Fuchsia*. In both groups, polyploidy is associated with 3-aperturate pollen, considered to be derived from the more common 2-aperturate condition in the genus (Nowicke et al., 1984). Despite differences between the two sections in viscin thread type (Nowicke et al., 1984), seed number and anatomy, sexual systems, and other morphological features (Berry, 1982), a

under cultivation is not known, but the extent of the two different chromosome numbers needs to be examined further in nature. Cases of intraspecific polyploidy are widespread in the Onagraceae and have been recorded in over 40 species and 11 genera (Lewis, 1979).

The high level of pollen abortion in the artificial hexaploid between a tetraploid and an octoploid subspecies of *Fuchsia regia* is indicative of irreg——, B. A. STEIN, S. CARLQUIST & J. W. NOWICKE. 1988. *Fuchsia pachyrrhiza*, a new tuberous species and section of *Fuchsia* from northwestern Peru. Syst. Bot. 13: 483–492.

BREEDLOVE, D. E. 1969. The systematics of Fuchsia sect. Encliandra (Onagraceae). Univ. Calif. Publ. Bot. 53: 1-69.

——, P. E. BERRY & P. H. RAVEN. 1982. The Mexican and Central American species of *Fuchsia* (Onagraceae) except for sect. *Encliandra*. Ann. Missouri Bot. Gard. 69: 209-234.

ularities in meiotic pairing and disjunction, which may explain the absence of naturally occurring hexaploids among the individuals sampled in areas where tetraploids and octoploids both were found. Areas where tetraploid and octoploid populations of *F. regia* are known to occur sympatrically, such as the Serra da Bocaina and Campos do Jordão in northern São Paulo state, and the Itatiaia massif and the Serra dos Órgãos in Rio de Janeiro, should be sampled more intensively for naturally occurring hexaploids.

Within the Onagraceae, the pattern of polyploidy in *Fuchsia* sect. *Quelusia* is most similar to that of *Ludwigia*, where polyploidy has been a frequent and important part of the evolutionary strategy in most of the genus, with numerous cases of intraspecific polyploidy (Raven & Tai, 1979). Unlike the situation in tribe Onagreae, where polyploidy is associated with autogamy and aneuploidy in annual species, aneuploidy is unknown in *Fuchsia* and *Ludwigia*, and polyploid taxa are perennial and predominantly outcrossing. This clearly shows that the effects of polyploidy can vary widely in related genera, depending on factors such as the longevity of the species and the habitat in which they occur.

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1534.

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APPENDIX I. Chromosome numbers in Fuchsia sects. Quelusia and Kierschlegeria.⁴

Fuchsia alpestris Gardner. Populations with n = 22. BRAZIL. RIO DE JANEIRO: Teresópolis, Berry et al. 4418. Fuchsia alpestris Gardner. Populations with n = 44. CULTIVATED: The Netherlands, from plants long in cultivation in Europe, Berry & Brako 001-86.

⁴ All counts were meiotic, except somatic counts indicated by "2n." Counts of Ramamoorthy collections were made by T. P. Ramamoorthy. Peter Raven counted both plants of *F. lycioides*; all other counts were made by the authors, except those with a cited reference. Only confirmed literature reports with vouchers or identifiable photographs were included. Unless otherwise indicated, voucher specimens are at the Missouri Botanical Garden (MO).

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Fuchsia bracelinae Munz (n = 22).

BRAZIL. ESPÍRITO SANTO: Pico da Bandeira, Berry et al. 4524, 4535. MINAS GERAIS: Pico da Bandeira, Berry et al. 4531.

Fuchsia brevilobis P. Berry (n = 22).

BRAZIL: SÃO PAULO: 38 km NE of São Paulo-Paraná border, on Hwy. BR-116, *Davidse et al. 10902* (n = 22, 2n = 44). PARANÁ: Mun. Bocaiúva do Sul, 3 km W of Sesmaria, *Berry & Juarez 4441*; Mun. Morretes, Porto de Cima, *Berry & Juarez 4495*; above Prainhas,

Quellón, Marticorena & Quezada 1694 (2n = 44); Dalcahue, Castro to Ancud, Marticorena & Quezada 1696 (2n = 44); Estero Mechaico to Río San Antonio, Castro to Ancud, Marticorena & Quezada 1698 (2n = 44);Chamiza, Prov. Llanquihue, Marticorena & Quezada 1699 (2n = 44); 2 km from Correntoso to Lago Chapo, Marticorena & Quezada 1703 (2n = 44); Lago Chapo, Marticorena & Quezada 1704 (2n = 44); Santa Ida, Lago Llanquihue, Marticorena & Quezada 1706 (2n = 44); Puerto Varas to Ensenada, Lago Llanquihue, Marticorena & Quezada 1707 (2n = 44); Saltos de Petrohué, Parque Nacional Vicente Rosales, Marticorena & Quezada 1708 (2n = 44); Petrohué, Lago Todos Los Santos, Marticorena & Quezada 1709 (2n = 44); Río Cruzes, S of Lanco, Prov. Valdivia, Marticorena & Quezada 1711 (2n = 44); Lastarria, Río Cautín, Prov. Cautín, Marticorena & Quezada 1712 (2n = 44); 5 km S of Lautaro, Prov. Cautín, Marticorena & Quezada 1713 (2n = 44); Corral, Valdivia, Godoy s.n. (2n = 44). MA-GALLANES (XII Región): Punta Hatley, Seno Otway, Pisano s.n. (2n = 44); Fuerte Bulnes, Magellan Straits, $Pisano \ s.n. \ (2n = 44).$ CULTIVATED: Ireland, Nelson 576 (2n = 44), 1162 (2n = 44, previously living at MO); California, at Univ. California Botanic Garden, Berkeley (n = 22, 2n = 44;Kurabayashi et al., 1962); Germany (n = 22; photograph in Warth, 1925, as "F. coccinea").

Cordeiro et al. 215 (MBM); below Estação Eng. Lange, road to Prainhas, Cordeiro et al. 218 (MBM); Mun. Antonina, Cacatu, Hatschbach et al. 50788 (MBM).

Fuchsia campos-portoi Pilger & Schulze (n = 22).

BRAZIL: RIO DE JANEIRO: Itatiaia, Berry et al. 4435, Ramamoorthy & de Lima s.n.

Fuchsia campos-portoi \times F. regia subsp. regia (natural hybrid, n = 22).

BRAZIL: RIO DE JANEIRO: Itatiaia, Berry et al. 4440.

Fuchsia coccinea Dryander (n = 22).

BRAZIL: MINAS GERAIS: Serra da Piedade, Berry et al. 4553, 4558.

Fuchsia glazioviana Taubert (n = 22).

BRAZIL: RIO DE JANEIRO: Morro da Nova Caledônia, Nova Friburgo, *Berry et al. 4423*, 4430 (probable introgressive hybrid with *F. regia* subsp. *regia*).

Fuchsia hatschbachii P. Berry (n = 22).

BRAZIL: PARANÁ: Mun. Campo Largo, Serra São Luis

Fuchsia regia (Vellozo) Munz subsp. regia. Populations with n = 22.

BRAZIL: RIO DE JANEIRO: Morro da Nova Caledônia, Nova Friburgo, Berry et al. 4425, 4433, 4424 (probable hybrid with F. glazioviana); Itatiaia, road to Planalto, Berry et al. 072, 074, 076, 082. MINAS GERAIS: Tronqueiras to Vale Verde, Alto Caparaó, Berry et al. 4543; Serra do Itacolomi, Ouro Preto, Berry et al. 4544, 4546 (probable introgressive hybrid with F. coccinea). SÃO PAULO: 17 km SE of Campos do Jordão, Ramamoorthy 683 (2n = 44); Campos do Jordão, Berry et al. 089, 090, 091; Serra da Bocaina, Berry et al. 083, 085. CULTIVATED: The Netherlands, from seed of Berry 4425, from Rio de Janeiro, Brazil, Berry & Brako 019-86.

do Purunâ, Berry et al. 4458, 4461; Mun. Bocaiúva do Sul, Bacaetava, Kummrow et al. 2998 (MBM).

CULTIVATED: The Netherlands, from seed of Berry 4464, from Paraná, Brazil, Berry & Brako 008-86.

Fuchsia lycioides Andrews (n = 22).

CULTIVATED: University of California Botanical Garden, Berkeley, UCBG # 53.1303-S2, from seed of Hartwig in 6 Oct. 1953, from Punta Molles, Chile; University of California at Los Angeles, seedling from seed collected by D. M. Moore in Coquimbo, Chile (2n = 44; without voucher).

Fuchsia magellanica Lamarck (n = 22).

ARCENTINA: NEUQUÉN: Villa Angostura, Nahuel Huapi, Diem 3614 (2n = 44), 3615 (2n = 44).

CHILE. BÍOBÍO (VIII Región): Concepción, Barrio Universitario, Riquelme s.n. (2n = 44); Las Canoas, Concepción to Chaimavida, Riquelme s.n. (2n = 44). LOS LAGOS (X Región): S of Valdivia, Marticorena & Quezada 1671 (2n = 44), 1672 (2n = 44); Puente Rahue, Prov. Osorno, Marticorena & Quezada 1676 (2n = 44); Frutillar Bajo, Prov. Llanquihue, Marticorena & Quezada 1677 (2n = 44); Frutillar Bajo to Frutillar Alto, Marticorena & Quezada 1678 (2n = 44); 2 km W of Llanquihue, Marticorena & Quezada 1679 (2n = 44); 24 km S of Puerto Montt, Marticorena & Quezada 1680 (2n = 44); El Avellanal, 8 km from Pargua, Marticorena & Quezada 1682 (2n = 44); Prov. Chiloé, Chacao to Ancud, Marticorena & Quezada 1683 (2n = 44); Paranqui to Curamo, Chiloé, Marticorena & Quezada 1684 (2n = 44); 4 km from Castro to Quellón, Chiloé, Marticorena & Quezada 1686 (2n = 44), 1687 (2n = 44); Lago Natri, Chiloé, Marticorena & Quezada 1689 (2n = 44); Rio Mollueco, Castro to Quellón, Marticorena & Quezada 1692 (2n = 44); 3 km past Coinco Alto, Castro to Quellón, Marticorena & Quezada 1693 (2n = 44);

Fuchsia regia (Vellozo) Munz subsp. regia. Populations with n = 44.

BRAZIL. RIO DE JANEIRO: Teresópolis, Berry et al. 4419; Itatiaia, Planalto, Berry et al. 4439; Serra dos Órgãos, Falkenberg & al. 3743 (FLOR). SÃO PAULO: Campos do Jordão, Ramamoorthy & Vital 673, 676, 680; Serra da Bocaina, Ramamoorthy & de Lima 1178.

Fuchsia regia subsp. reitzii P. Berry (n = 44).

BRAZIL. SANTA CATARINA: Curitibanos, Berry & Falkenberg 4506 (multivalents common); Bom Jardim to São Joaquim, Berry & Falkenberg 4510 (multivalents common), 4513; Bom Jardim da Serra to Lauro Müller, Berry & Falkenberg 4517 (probable hybrid with F. regia subsp. serrae; multivalents common); Mun. Uribici, SW of Uribici, Falkenberg et al. 3777 (FLOR). RIO GRANDE DO SUL: E of Tainhas on RS-486, Falkenberg et al. 3746 (FLOR); Posto Fiscal, W of Serra de Rocinha, Falkenberg et al. 3767 (FLOR).

CULTIVATED: The Netherlands, from seed of Berry & Falkenberg 4510, from Santa Catarina, Brazil, Berry & Brako 013-86.

Fuchsia regia subsp. serrae P. Berry (n = 44). BRAZIL: SÃO PAULO: road between Mogi das Cruzes and

Bertioga, Pirani & Yano 640 (SP). PARANÁ: Mun. Bocaiúva do Sul, 9 km W of Sesmaria, Berry & Juarez 4448 (possible hybrid with F. brevilobis); 12 km W of Sesmaria, Berry & Juarez 4450; Estrada da Graciosa, Mun. Morretes, Berry et al. 4492 (multivalents common), 4493; Mun. Morretes, Ramamoorthy & Hatschbach 829 (n = 44, 2n = 88), 830. SANTA CATARINA: Rio do Sul to Curitibanos, Berry & Falkenberg 4501 (multivalents common); from Taimbezinho to Praia Grande, Falkenberg et al. 3752 (FLOR); 13 km above Timbé do Sul, below Serra da Rocinha, Falkenberg et al. 3753 plants intermediate between subsp. regia and subsp. serrae (n = 22, 44).

BRAZIL. RIO DE JANEIRO: above Parati to Cunha, Berry et al. 097 (n = 44), 100 (n = 22). SÃO PAULO: Alto da Serra, W of Ubatuba, Berry et al. 095 (n = 22), 096 (n = 44); Alto da Serra, above Caraguatatuba, Berry et al. 092 (n = 22), Ramamoorthy & Vital 688 (n = 44, previously living specimen at MO); Serra da Bocaina, Ramamoorthy & de Lima 1176 (n = 44).

Fuchsia regia subsp. regia × F. regia subsp. serrae (2n - 66)

(FLOR). RIO GRANDE DO SUL: 20 km E of Tainhas on RS-486, Falkenberg et al. 3744 (FLOR).

CULTIVATED: The Netherlands, from seed of *Berry* 4450, from Paraná, Brazil, *Berry & Brako 023-86*; the Netherlands, from seed of *Berry* 4504, from Santa Catarina, Brazil, *Berry & Brako 024-86*.

Fuchsia regia: plants intermediate between subsp. regia and subsp. serrae (n = 22, 44). = 66).

Artificial hybrid between Ramamoorthy 683 (subsp. regia, n = 22) and Ramamoorthy & Hatschbach 830 (subsp. serrae, n = 44), cultivated at Missouri Botanical Garden, M2588.